Increased snow facilitates plant invasion in mixedgrass prairie

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Summary

• Although global change is known to influence plant invasion, little is known about interactions between altered precipitation and invasion. In the North American mixedgrass prairie, invasive species are often abundant in wet and nitrogen (N)-rich areas, suggesting that predicted changes in precipitation and N deposition could exacerbate invasion.

• Here, this possibility was tested by seeding six invasive species into experimental plots of mixedgrass prairie treated with a factorial combination of increased snow, summer irrigation, and N addition.

• Without added snow, seeded invasive species were rarely observed. Snow addition increased average above-ground biomass of *Centaurea diffusa* from 0.026 to 66 g m^{-2}, of *Gypsophila paniculata* from 0.1 to 7.3 g m^{-2}, and of *Linaria dalmatica* from 5 to 101 g m^{-2}. Given added snow, summer irrigation increased the density of *G. paniculata*, and N addition increased the density and biomass of *L. dalmatica*. Plant density responses mirrored those of plant biomass, indicating that increases in biomass resulted, in part, from increases in recruitment. In contrast to seeded invasive species, resident species did not respond to snow addition.

• These results suggest that increases in snowfall or variability of snowfall may exacerbate forb invasion in the mixedgrass prairie.

Introduction

Invasive weeds threaten the economic productivity and biological diversity of rangeland ecosystems (DiTomaso, 2000). In contrast to weed control in cropping systems, where herbicides are cost-effective, successful control of invaders over vast acreages of rangeland depends on the ability of rangelands to resist invasion (Masters & Sheley, 2001; Levine *et al.*, 2004). Unfortunately, global change alters the environment, often decreasing its suitability for native species (Alpert, 2006; Facon *et al.*, 2006), and increasing the availability of plant resources (Davis *et al.*, 2000; Blumenthal,

2005). Both types of change threaten to increase invasibility of native plant communities (Dukes & Mooney, 1999; Walther *et al.*, 2002). Therefore, to effectively predict how global changes will influence rangeland ecosystems, we need to understand how they will influence invasion.

Many global anthropogenic changes have the potential to influence the success of invasive plant species relative to native plant species (Dukes & Mooney, 1999; Vila *et al.*, 2007). Some changes tend to facilitate invasion, such as nutrient enrichment and disturbances associated with altered land use (Huenneke *et al.*, 1990; Hobbs & Huenneke, 1992; Bobbink *et al.*, 1998; Daehler, 2003). Increases in atmospheric carbon

dioxide concentrations can also enhance the growth of invasive species, often more than they enhance growth of coexisting native species, but the generality of these patterns remains unclear (Dukes, 2000; Smith *et al.*, 2000; Hättenschwiler & Körner, 2003; Weltzin *et al.*, 2003; Ziska, 2003; Belote *et al.*, 2004; Nagel *et al.*, 2004). Experimental warming facilitates invasion by C_4 annuals in New Zealand (White *et al.*, 2001) and recent warming appears to have allowed invasion by broadleaf evergreen species in Swiss forests (Walther, 2003).

Relatively little is known about how changes in precipitation may influence invasion (Vila *et al.*, 2007), in part because changes in precipitation are themselves difficult to predict. The average global surface air temperature has increased approx. 1°C in the past century, and is expected to increase an additional approx. 3°C over the next century (Meehl *et al.*, 2007). As a result, more frequent and severe heatwaves are predicted, plus higher atmospheric humidity and a more dynamic hydrological cycle, including more intense storms, and increased risk of drought. For North America, annual mean precipitation is predicted to increase in most regions, especially in winter and early spring, and most notably in the northeastern USA and southern Canada (Christensen *et al.*, 2007).

Although responses of invasive species to a given change in precipitation are also likely to vary, there are reasons to expect that increases in precipitation may exacerbate invasion (Dukes & Mooney, 1999). The fluctuating resource hypothesis suggests that both increases in precipitation and increases in the variability of precipitation could increase water availability, and therefore invasion (Davis *et al.*, 2000). Invasive species will be most likely to benefit from increased water availability if they have high water requirements relative to native species. Traits that may lead to high water requirements include fast growth rates (Capin, 1980) and short life spans, which necessitate frequent recruitment. These traits are typical of opportunistic species (Grime *et al.*, 1997, Daehler, 1998), and are common among invasive species (Rejmanek & Richardson, 1996; Cadotte & Lovett-Doust, 2001; Grotkopp *et al.*, 2002; Leishman *et al.*, 2007). The prediction that increases in precipitation will increase invasion is in accordance with observations of high invasive species richness or abundance in wet areas or years (Stohlgren *et al.*, 1998; Hood & Naiman, 2000; Larson *et al.*, 2001; Reever Morghan & Rice, 2006), and an increasing number of experimental studies that have found that water addition increases invasion (Milchunas & Lauenroth, 1995; Davis & Pelsor, 2001; White *et al.*, 2001; Goergen & Daehler, 2002; Miller *et al.*, 2006; Thomsen *et al.*, 2006; Garcia-Serrano *et al.*, 2007). Water addition does not always lead to invasion, however, and its net effect on invasion may often depend on the timing of precipitation relative to the phenology of both native and invasive species (Walker *et al.*, 2005; James *et al.*, 2006; Renne *et al.*, 2006).

The mixedgrass prairie is the largest remaining native grassland in the Great Plains, covering 142.7×10^4 km^2 and representing 38% of the grassland area in North America

(Lauenroth, 1979). Predicted increases in storm intensities and changes in precipitation dynamics (Christensen *et al.*, 2007; Meehl *et al.*, 2007) are expected to cause shifts in the plant community composition (Knapp *et al.*, 2002), and may present opportunities for invasion (Weltzin *et al.*, 2003). Given patterns of high invasive species richness and abundance in riparian areas within the mixedgrass prairie (Stohlgren *et al.*, 1998; Larson *et al.*, 2001), periods of increased soil moisture might be expected to increase invasion. Altered precipitation may be most likely to increase invasion in conjunction with increased nitrogen (N) deposition, which has been observed in many areas within the mixedgrass prairie (Kochy & Wilson, 2001). If such changes do lead to invasion, the consequences could be severe. Weed invasion in the mixedgrass prairie threatens both rural communities and biological diversity (Stohlgren *et al.*, 1998; DiTomaso, 2000). For example, invasive *Centaurea* species can reduce forage for both livestock and wildlife, and have been estimated to cost Montana livestock producers \$42 million yr^{-1} (Trammell & Butler, 1995; Hirsch & Leitch, 1996).

Nevertheless, there are no field manipulation studies in the mixedgrass prairie that address how changes in climate will affect the invasibility of this region. The objective here was to quantify the interactive effects of increases in winter snow, summer rainfall, and N on the success of six invasive species.

Materials and Methods

Study site

Our study was conducted at the USDA-ARS High Plains Grassland Research Station (HPGRS) west of Cheyenne, Wyoming, USA. HPGRS is located at 1930 m at the southern end of the mixedgrass prairie of North America (41°N, 104°W). Mean annual precipitation at HPGRS is 38 cm with an average of 127 frost-free d yr^{-1}. The average summer temperature is 18°C and the average winter temperature is −2.5°C. The major cool-season (C_3) grasses are *Pascopyrum smithii* (Rydb.) A. Love (western wheatgrass), and *Stipa comata* (needle-and-thread) Trin & Rupr. The dominant warm season (C_4) grass is *Bouteloua gracili*s (H.B.K.) Lab. Ex Steud (blue grama). The vegetation also contains a wide variety of forbs and subshrubs. The soils are mixed, mesic, Aridic Argiustolls, and the soil series is an Ascalon sandy loam (Schuman *et al.*, 1999). Our study was limited to the Ascalon soil type. During the 8 yr before the study, the site was grazed at a moderate stocking rate of 6.29 ha per cow–calf pair. Cattle were excluded from the area during the study.

Experimental design and treatment application

To examine the effects of altered precipitation and N deposition on invasion, we seeded invasive species into plots of intact grassland treated with a factorial combination of snow-addition,
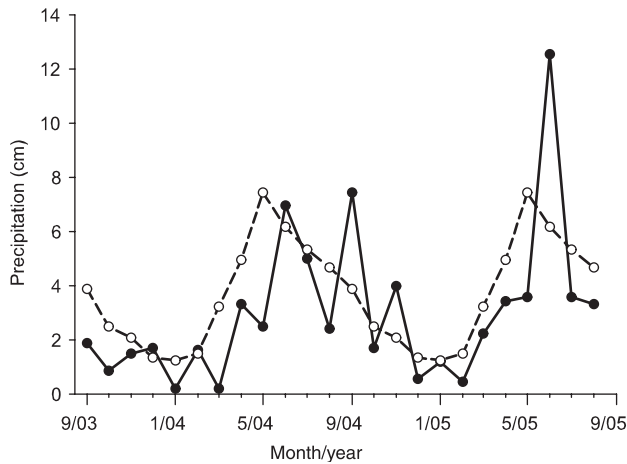
Fig. 1 Monthly precipitation at the High Plains Grassland Research Station (Wyoming, USA) during the study (closed circles) and averaged over the 28 yr before the study (open circles).

summer-irrigation, and N addition. Treatments were arranged in a split-split plot design, with two levels of snow in whole plots, two levels of irrigation in subplots, two levels of N in sub-subplots, and three replications. Irrigation and N addition treatments were randomly assigned to subplots and sub-subplots, respectively. Each sub-subplot was 2.95 × 1 m, and comprised two treated areas, each 1.3 × 1 m, separated by a 0.35 m walkway. Irrigation subplots were separated by 1 m buffer zones of intact prairie. N addition sub-subplots were separated by 0.35 m buffer zones of intact prairie.

We increased snow using three snow fences, 1 m high by 25 m long, constructed of commercially available lath fencing, oriented perpendicular to the prevailing winter winds. High snow plots were located 1 m to the leeward side of the fence, in the zone of maximum snow accumulation. Average midwinter snow depth behind the fences was 50 cm, which would be expected to yield an average snow water equivalent of 26 cm. Ambient snow plots were located 20 m to the windward side of the snow fence, to avoid any influence of the fence on snow accumulation. Fences were removed during the growing season. Summer precipitation was increased by adding 50% of the 30 yr average monthly precipitation. We applied water in weekly increments from mid-May through mid-August. Owing to a calculation error, we applied only 25% of the 30 yr average during the first month of watering in 2005. Fortuitously, this error coincided with unusually high natural precipitation (Fig. 1), and is unlikely to have strongly influenced the outcome of the irrigation treatment. Water was applied by hand, with a watering wand attached to a hose and a battery-powered pump. Nitrogen was increased by adding 2.63 g m^{-2} of N annually, as 33.5-0-0 ammonium nitrate fertilizer. These rates are similar to the highest rates of N deposition observed by Kochy & Wilson (2001) in a survey of the Canadian mixedgrass prairie. We applied fertilizer in four increments in April 2004, August 2004,

May 2005, and July 2005. At each date, 10.2 g of fertilizer was dissolved in 0.5 l of water, and sprayed on using a handheld sprayer. Nonfertilized plots were sprayed with an equivalent amount of water.

Study species and seed addition

Six invasive species were seeded into all plots: *Bromus tectorum* L. (cheatgrass), *Centaurea diffusa* Lam. (diffuse knapweed), *Cirsium arvense* (L.) Scop. (Canada thistle), *Euphorbia esula* L. (leafy spurge), *Gypsophila paniculata* L. (baby's breath), and *Linaria dalmatica* (L.) P. Mill. (Dalmatian toadflax). We chose these species both because they were present on mixedgrass prairie at HPGRS, and because they are all capable of invading intact grassland. All of the species except for *B. tectorum* and *G. paniculata* are listed as noxious weeds in Wyoming (http://plants.usda.gov). *Bromus tectorum* is among the most problematic weeds in North America, occupying 40 million ha in the western United States (DiTomaso, 2000). *Gypsophila paniculata* is listed as a noxious weed in California and Washington State. It was planted at HPGRS as an ornamental and is now invading adjacent prairie.

Invasive species were planted in rows, oriented perpendicular to the snow fence, to facilitate finding and repeatedly measuring seedlings. We seeded each species within two randomly located 100 cm strips (11.66 cm strip widths) within each subplot, resulting in two 70 × 100 cm seeded areas in each subplot. Seeded areas were surrounded by 30 cm buffer areas that received the same treatment as seeded areas. To facilitate germination and establishment, half of each strip (5.83 × 100 cm) was disturbed to a depth of 3 cm using a pointed hoe. A quantity of 0.6 g of seed from a single species was added to each strip in late November 2003. The number of seeds added to each strip therefore varied by species, and was approx. 297 for *B. tectorum*, 545 for *C. diffusa*, 659 for *C. arvense*, 194 for *E. esula*, 1290 for *G. paniculata*, and 5217 for *L. dalmatica*.

Measurement of soil water, plant density and plant biomass

We measured volumetric water content of precipitation (but not N) treatments using vertically inserted, 30-cm-deep CS616 time-domain reflectometry probes attached to a CR10X data logger (Campbell Scientific, Logan, UT, USA). We placed probes in all subplots within two of the three replicates, for a total of eight probes. Probes were installed in the center of each subplot, outside of areas planted with weeds, and therefore measured the effects of precipitation treatments in the absence of invasion. We calibrated the probes using field measurements of gravimetric water contents collected over the course of the study.

We counted emerged seedlings of each invasive species in early April, early May, late June and late Septemper 2004.

Invasive species were counted for a final time and harvested between 28 July and 2 August 2005. In one of the whole plots, an extant population of *L. dalmatica* compromised our identification of seeded plants of the same species. For this species, therefore, only two whole plots were harvested. Resident species within seeded areas were harvested immediately following the invasive species harvest. We clipped all remaining plants in one randomly located 50×37.5 cm frame within each planted area, and separated them into monocots and dicots. All plants were dried at 60°C for 3 d before weighing.

Data analysis

All analyses were conducted in JMP version 5 (SAS Institute, 2002). Where necessary, data were transformed to reduce heteroscedasticity, using either log_{10} or square root transformations. Soil water data, which did not include the N treatment, were analyzed using a split-plot, repeated-measures ANOVA, including snow, irrigation, date and appropriate interactions, with replication, replication × snow, and replication × snow × irrigation as random effects. Split-split ANOVAs for biomass of resident monocots and dicots included replication, snow, irrigation, N and interactions, with replication, replication × snow, and replication × snow × irrigation as random effects.

Because added invasive species were largely absent from plots without added snow, resulting in a large number of zeros, effects of snow on invasive species biomass and density were tested using a Welch's nonparametric *t*-test. Effects of irrigation and N on invader biomass within added snow plots were tested using split-plot ANOVAs including irrigation, N, and interactions, with replication and replication × irrigation as random effects. Effects of irrigation and N on invader numbers within added snow plots were tested using split-plot repeated-measures ANOVAs that included irrigation, N, date, and interactions, with replication, replication × irrigation, and replication × irrigation × N as random effects. In all split-plot ANOVAs, we ensured that appropriate error terms (see the Results section for degrees of freedom) were used to test for whole-plot and subplot effects. For example, in analyses involving all treatments, replication × snow and replication × snow × irrigation formed the denominators for *F*-statistics used to test effects of snow and irrigation, respectively. Similarly, in repeated-measures analyses including only irrigation and N treatments, replication × irrigation and replication × irrigation × N were used to test effects of irrigation and N, respectively.

Results

Precipitation and soil water content

Over the course of the experiment, from November 2003 to August 2005, ambient annual precipitation was 84% of the long-term average for the research station (Fig. 1). November–April precipitation was 60% of average in 2003–04, and 83% of average in 2004–05. May–October precipitation in 2004 was 87% of average, and May–August precipitation in 2005 was 98% of average.

Snow and irrigation treatments functioned as expected. During winter 2003–04, snowdrifts formed in early December and melted by early March. In winter 2004–05 drifts formed in November and melted by April. Of the two replications instrumented with TDR probes, one frequently failed to yield data. Consequently, statistical analyses are limited to the period for which we have data from all eight probes, between 20 April and 16 June 2004. Within this period, both snow fences and irrigation increased soil water content ($F_{1,1} = 443$, $P = 0.030$; $F_{1,1} = 569$, $P = 0.027$, respectively) with the magnitude of these effects varying with date (date × snow, $F_{1,452} = 100$, $P < 0.0001$; date × irrigation, $F_{1,452} = 82$, $P = P < 0.0001$). Trends in soil water content across both growing seasons suggest that effects of snow were particularly strong early in the 2004 growing season, while irrigation effects were strongest during the driest parts of each growing season (Fig. 2).

Plant biomass and density

Of the six planted invaders, only *C. diffusa*, *G. paniculata*, and *L. dalmatica* successfully invaded the plots, leading to populations that persisted (because of regrowth or germination following plant harvest) 3 and 4 yr after the initial seeding. We therefore present results for these species only. Of the remaining species, *B. tectorum* and *E. esula* showed patterns of emergence that were qualitatively similar to those described later for the successful invaders (data not shown); *C. arvense* seedlings were only rarely observed.

Planted invaders attained little or no biomass in plots without added snow. Average biomasses of *C. diffusa*, *G. paniculata*, and *L. dalmatica* in control plots were 0.04, 1.4, and 2.2% of those in snow addition plots, respectively ($P < 0.01$ in all cases; Fig. 3). In plots with added snow, N addition and irrigation also influenced invader biomass, but effects were less consistent than those observed for the snow treatment (Fig. 3). Nitrogen addition increased biomass of *L. dalmatica* ($F_{1,4} = 102$, $P = 0.0097$). Irrigation led to a marginally significant increase in *G. paniculata* biomass ($F_{1,2} = 16.6$, $P = 0.055$). No significant interactions were observed between N addition and irrigation.

Precipitation and N treatments influenced the final density of invaders in much the same way as they influenced invader biomass. Invaders were rarely observed in plots without added snow (Fig. 4). Addition of snow increased the final per-plot density of all three invaders, from less than one to 37 plants of *C. diffusa*, from less than one to 24 plants of *G. paniculata* and from nine to 69 plants of *L. dalmatica* ($P < 0.02$ in all cases). Given added snow, N addition increased the final
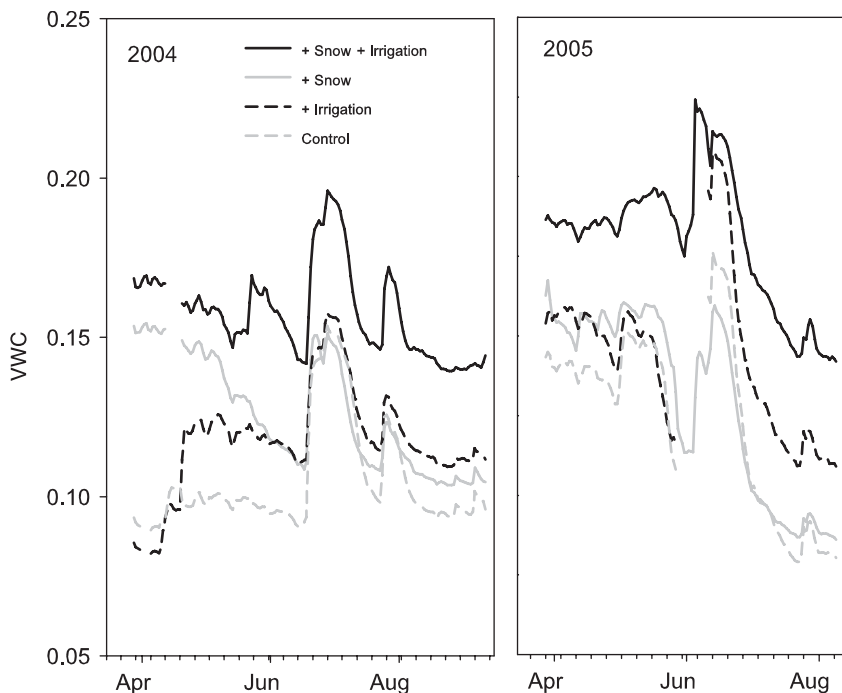
Fig. 2 Soil volumetric water content (VWC) as a function of winter and summer precipitation treatments during the 2004 and 2005 growing seasons.
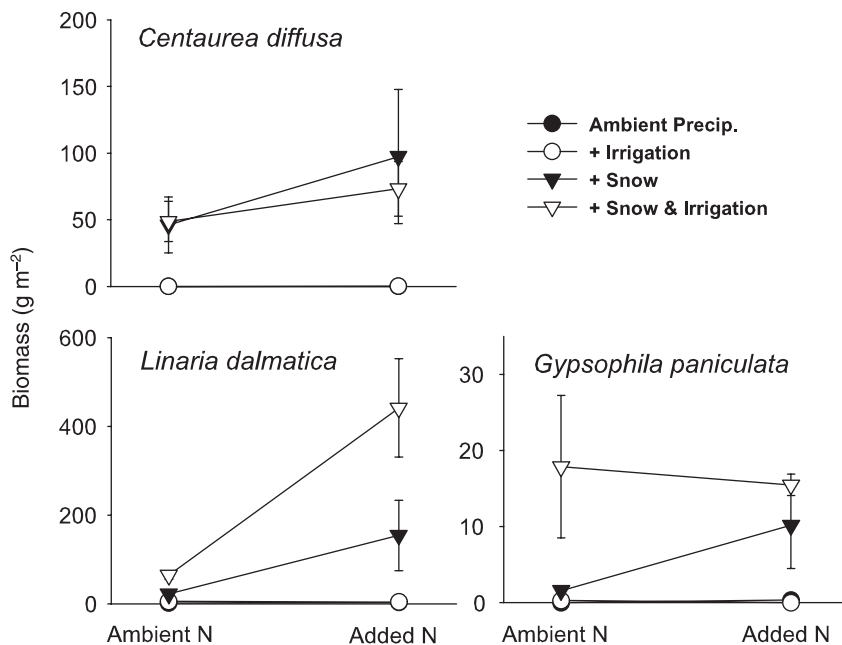

Fig. 3 Above-ground biomass of seeded invaders in plots with and without added snow, summer irrigation or nitrogen (N). Significant increases in biomass were observed for all species with snow addition, and for *Linaria dalmatica* with N addition.

density of *L. dalmatica* from 37 to 101 seedlings per plot ($F_{1,4}$ = 54.3, P = 0.018), and irrigation increased density of *G. paniculata* from 12 to 36 seedlings per plot ($F_{1,2}$ = 342, P = 0.0029). Analyses of plant density including all five survey dates showed no effects of N or irrigation. Density was influenced by date for all three invaders, however ($P < 0.001$ in all cases; Fig. 4). In particular, invader density decreased dramatically between early May and early July of 2004. In contrast to plant density, the average size of invasive plants was

not significantly influenced by irrigation or N addition in added-snow plots. This negative result should be interpreted with caution, however, as we did observe nonsignificant trends towards increased plant size with these treatments, and the experiment had limited power to test for such effects.

Total plant biomass, including both resident species and added invaders, increased with both snow ($F_{1,2}$ = 63.3, P = 0.015) and N addition ($F_{1,8}$ = 6.88, P = 0.031; Fig. 5). Of the increase in biomass from the snow treatment, 50% was
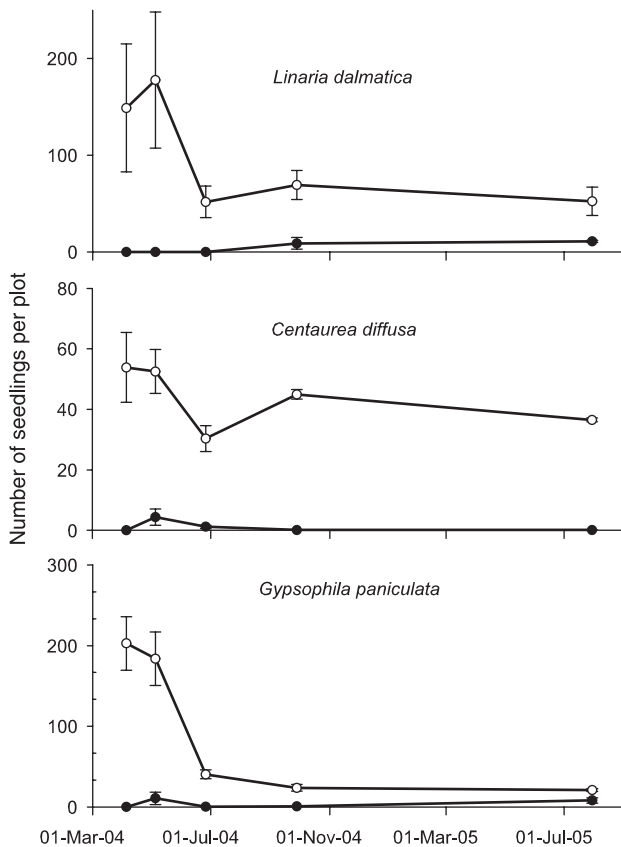
Fig. 4 Changes in invasive species density over the course of the experiment in plots with added snow (open symbols) and ambient snow (closed symbols), averaged across irrigation and nitrogen (N) treatments.
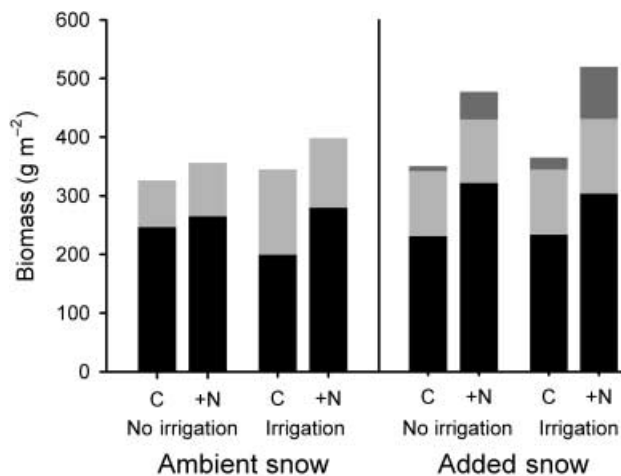

Fig. 5 Total above-ground biomass in late July 2005. Significance of treatment effects varied with plant group (resident monocots, black bars; invasive dicots, dark grey bars; resident dicots, light grey bars). Snow addition and nitrogen (N) addition increased total biomass and biomass of added invasive dicots; irrigation increased biomass of resident dicots, and N addition increased biomass of resident monocots.

accounted for by invasive species biomass. Resident monocots, including grasses and sedges, increased only with N addition ($F_{1,8}$ = 8.55, P = 0.019), while resident dicots, including forbs and subshrubs, increased only with irrigation ($F_{1,4}$ = 17.2, P = 0.014). We found no significant interactions among treatments for any of the plant groups.

Discussion

Within the mixedgrass prairie, invasive forbs are often most abundant in riparian areas, suggesting that high water availability may be necessary for successful invasion (Stohlgren *et al.*, 1998; Larson *et al.*, 2001). Our experimental results confirm the importance of water, particularly winter precipitation, to mixedgrass prairie invasion. We found virtually no invasion without increased snow, but successful invasion by three invasive forbs, *C. diffusa*, *L. dalmatica*, and *G. paniculata*, with increased snow (Fig. 3).

In contrast to seeded invasive species, resident vegetation was not influenced by snow (Fig. 5). The resident vegetation was dominated by native species, primarily established perennials. Monocots responded to N addition and dicots responded to summer irrigation. The fact that total biomass, including invasive weeds, did increase with addition of snow suggests that invasive species may have exploited resources that otherwise would have enabled resident vegetation to respond to snow. Alternatively, the lack of a snow effect may have been specific to 2005. In adjacent, nonseeded plots, snow increased total biomass in 2003 and 2004, but not 2005 (R. A. Chimner *et al.*, unpublished). Irrespective of the degree of competition between resident and seeded species, however, seeded invasive species responded much more strongly to increased snow than did resident species. This suggests that high snowfall may increase the success of invasive relative to native species.

Several mechanisms might explain the strong response of invasive species to increased snow in this experiment. First, water availability is often particularly important during recruitment. Short-lived invasive forbs must recruit more frequently than the longer-lived species against which they must compete to invade mixedgrass prairie. Consequently, environments that favor recruitment, even if they favor recruitment of all species equally, may also facilitate invasion. The sensitivity of recruitment to water stress has been observed in grasslands in general (Lauenroth *et al.*, 1994; Foster & Dickson, 2004), and with respect to invasive species in particular (Goergen & Daehler, 2002; Miller *et al.*, 2006; Thomsen *et al.*, 2006). In this experiment, added snow increased water supply at a time of low plant water use, and led to extended periods with high soil water content (Fig. 2). We observed few seedlings of any of the invasive species without added snow (Fig. 5). Furthermore, even with added snow, all three invasive species suffered considerable mortality as soil water declined from early May to late June in 2004. Increased recruitment appears to be at least partly responsible

for the increase in invasive species biomass with added snow, since treatment responses of invasive species numbers, but not per-plant biomass, mirrored those of invasive species biomass. It is important to note that the effect of snow on invasive species recruitment may have resulted, in part, from the relatively dry spring in 2004 (Fig. 1). Although it is difficult to guess how snow might have influenced recruitment in an average spring, it is clear that neither the relatively average precipitation during the subsequent fall and spring nor the irrigation treatment was sufficient for successful recruitment.

Increased snowfall might also have favored invasion by increasing the availability of deep relative to shallow soil water. Many invasive forbs, including those in this experiment, can develop deep tap roots, which may enable them to access water unavailable to relatively shallow-rooted species (Hill et al., 2006). Finally, increased snow could have favored the invasive species if they are poor competitors under conditions of limited water availability (Baruch & Fernandez, 1993; Thebaud et al., 1996). In performance comparisons between native and invasive species, invasive species tend to fare poorly with limited water availability (Daehler, 2003). By contrast, another recent study found no differences in water-use efficiency among 38 phylogenetically paired native and exotic species (Funk & Vitousek, 2007). Thus, while it is difficult to gauge whether differences in rooting depth or competitive ability contributed to invader responses to snow in our study, where these differences do occur, they might compound effects of snow on recruitment.

Effects of other treatments were less pronounced and less consistent among species, but suggest that, given sufficient snow, increases in summer rainfall or N deposition may also facilitate invasion (Fig. 3). Summer irrigation increased the abundance of G. paniculata. N addition increased the final abundance (from 37 to 101 plants per plot) and particularly the biomass (from 43 to 298 $g\,m^{-2}$) of L. dalmatica. The strength of this response suggests that where increases in winter precipitation coincide with increases in N deposition, they may dramatically increase invasion by L. dalmatica. Other species did not respond to irrigation and N addition, and no interactions were observed between irrigation and N addition. Given the limited power of the experiment, however, the absence of such effects should be interpreted with caution.

While invasion is a serious problem in parts of the northern mixedgrass prairie, the native grassland in much of this region remains relatively intact. The results of this study suggest that the ability of mixedgrass prairie to resist invasion may depend on limited snowfall. If climate change increases the frequency of wet winters in the mixedgrass prairie, it may also exacerbate invasion. The increase in snow in this experiment was larger than the average increase predicted to occur with climate change (Christensen et al., 2007); however, more frequent extreme precipitation events could still increase the frequency of very wet winters. This experiment suggests that such changes would enhance the recruitment, and therefore abundance, of invasive forbs. A key question in predicting the future vegetation dynamics of mixedgrass prairie is whether responses of established invasive forbs to changes in precipitation, and other global changes, will compound effects of precipitation on recruitment.

More broadly, this study supports suggestions that increases in precipitation may favor invasive over native species (Dukes & Mooney, 1999; White et al., 2001; Thomsen et al., 2006; Vila et al., 2007), and presents another example of how global change may contribute to invasion. In this example, the invasive species to benefit were short-lived perennial forbs, and their strong response to increased precipitation was mediated, at least in part, by increases in recruitment. Similarly, 5 yr of growing-season water addition led to long-term invasion by exotic annual and perennial forbs in the shortgrass steppe (Milchunas & Lauenroth, 1995). Water addition has also been found to increase recruitment of the winter-annual grass B. tectorum in arid grassland communities (Miller et al., 2006). Together, these experiments demonstrate that increases in precipitation in arid and semi-arid grasslands can allow opportunistic species, including many invasive species, to establish and grow in the face of competition from established native perennials. Similar results have been observed with respect to other global change factors that increase plant resource availability, including increases in N (Huenneke et al., 1990; Bobbink et al., 1998; Daehler, 2003), and atmospheric CO_2 (Smith et al., 2000; Hättenschwiler & Körner, 2003; Belote et al., 2004; Nagel et al., 2004). On balance, therefore, global change might be expected to favor opportunistic and invasive species adapted to high resource availability over native species adapted to low resource availability.

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